# Baleen whales and their prey in a coastal environment[1]

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Patterns of abundance of humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), and minke (*Balaenoptera acutorostrata*) whales are described in relation to the abundance of their primary prey, capelin (*Mallotus villosus*), during 1982–1985 at Witless Bay, Newfoundland. The abundance ratio of the three whale species was 10:1:3.5, respectively. Abundance of all whale species was strongly correlated with abundance of capelin through each season and between years. Capelin abundance accounted for 63% of the variation in whale numbers in 1983 and 1984, while environmental parameters (e.g., water temperatures) accounted for little variance. The amount of capelin consumed by whales was small (<2%) compared with the amount available. All three species overlapped temporally at Witless Bay, but spatial overlap was reduced as fins occurred primarily offshore, minkes primarily inshore, and humpbacks in bay habitats of intermediate depth.

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La densité des Rorquals à bosse (*Megaptera novaeangliae*) des Rorquals communs (*Balaenoptera physalus*) et des Petits Rorquals (*Balaenoptera acutorostrata*) a été étudiée en fonction de l'abondance de leur proie principale, le Capelan, *Mallotus villosus*, de 1982 à 1985, à Witless Bay, Terre-Neuve. Le rapport entre les densités respectives des trois espèces était de 10:1:3,5. La densité de chacune des espèces de rorquals était en corrélation très forte avec l'abondance des capelans durant toute la saison et à chaque année. L'abondance des capelans expliquait 63% de la variation du nombre de rorquals en 1983 et 1984 et les paramètres écologiques (p.e., température de l'eau) expliquaient peu de la variance. La quantité de capelans consommés était faible (<2%) comparativement à la quantité disponible. Il y avait chevauchement temporel des trois espèces à Witless Bay, mais le chevauchement spatial était moins important puisque les Rorquals communs se tenaient surtout au large, les Petits Rorquals plus près des côtes et les Rorquals à bosse, dans les habitats de profondeur intermédiaire.

[Traduit par la revue]

## Introduction

In April and May of each year, baleen whales gather to feed at productive offshore upswelling areas around the Grand Banks of Newfoundland (Parsons and Brownlie 1981). By June, many whales move inshore and migrate north along the coast, feeding opportunistically on dense schools of capelin (*Mallotus villosus*) and other prey (Whitehead 1981). A continuous turnover of foraging whales occurs over summer in locally productive coastal sites (Whitehead et al. 1980, 1982). Because of their numbers, large size, and high food demands, baleen whales may be important members of local food webs and potential competitors with seabirds, fish, and humans (Whitehead 1981; Hain et al. 1985).

A variety of schooling prey (e.g., sandlance (*Ammodytes* spp.), herring (*Clupea harengus*), euphausiids, and squid (*Illex* spp.)) are eaten by baleen whales, but their most important prey in eastern Newfoundland is capelin (Mitchell 1973, 1975). These small (ca. 15 cm) pelagic fish migrate inshore to spawn each summer in bays along the coast of Newfoundland, where they experience intense predation from whales, seabirds (Brown and Nettleship 1984), seals (Sergeant 1973), and fish, particularly cod (*Gadus morhua*; Methven and Piatt 1989).

In this paper, we describe patterns of abundance of baleen whales and capelin from May through August during 4 years (1982–1985) at a coastal area (30 km$^2$) centred in Witless Bay, Newfoundland. Variations in whale abundance were analyzed with respect to capelin abundance and environmental parameters. The amount of capelin consumed seasonally and annually by whales was estimated and compared with the amount of capelin estimated to be available in the study area, and with amounts taken by other predators.

## Study area and methods

This study was conducted in Witless Bay, on the eastern side of the Avalon Peninsula of Newfoundland (Fig. 1). Waters in and near Witless Bay are very productive in summer and support a large inshore cod fishery, as well as major breeding populations (Brown and Nettleship 1984) of Common Murres (*Uria aalge*), Atlantic Puffins (*Fratercula arctica*), and Black-legged Kittiwakes (*Rissa tridactyla*) on Gull, Green, and Great islands (Fig. 1). Local topographic features (islands, headlands, underwater shelves) and wind-induced coastal

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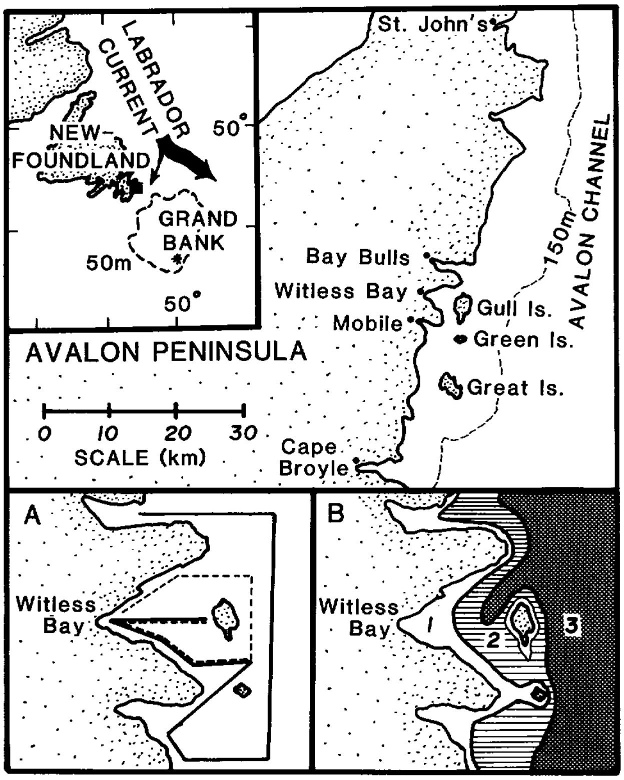


FIG. 1. Study area on the Avalon Peninsula of Newfoundland. Panel A shows the route taken on standardized hydroacoustic surveys in 1982 (broken line) and 1983–1984 (solid line). Panel B shows habitats: 1, <30 m, inshore; 2, 30–70 m, bay; and 3, >70 m, offshore. Asterisk on Grand Bank indicates location of Southeast Shoal.

upwelling serve to increase and localize productivity near shore (Piatt 1987; Schneider and Methven 1988).

Whales were observed from land and at sea from a 12-m research vessel (Table 1). Whales were observed opportunistically from vantage points on Gull Island in 1982–1984 (by A.E.B., R.L.M.). Standardized 1-h whale watches were conducted from Gull Island in 1985 (by E.C.). Whales were also observed (by J.F.P., D.A.M., V.M.) on standardized boat transects around Gull island (Fig. 1) in 1982–1984 during surveys for seabirds and capelin (Piatt 1987, 1989). Whale observations were later grouped according to three habitats (defined by bottom depths, Fig. 1) for analyses of spatial distributions: inshore (<30 m), bay (30–70 m), and offshore (>70 m).

Whale sightings were grouped into two data sets for analyses of temporal patterns of abundance. (*i*) Total numbers of whales observed per day: this data set combined observations from Gull Island and boat surveys, but duplicate sightings were discarded for analyses. (*ii*) Whales observed per hour of effort: this data set included only standardized whale observations from boat surveys in 1982–1984, and from Gull Island in 1985.

Estimates of relative capelin abundance were obtained from hydroacoustic surveys of the Witless Bay area (Fig. 1) as described in detail elsewhere (Piatt 1987, 1989). In brief, hydroacoustic echogram traces from a Skipper 609 (1982) or a Kelvin-Hughes Mark 2 (1983–84) echo sounder were partitioned over 250-m surface distance by 10-m depth intervals, and these blocks were graded (0–9) for fish registration intensity; intensities were squared and summed to yield an index of daily capelin abundance during the summers of 1982–1984 (Forbes and Nakken 1972; Piatt 1989). In 1985, echograms were obtained opportunistically from a charter vessel (Furuno Fishfinder) and were not graded for registration intensity. Instead, a relative index of capelin abundance in 1985 was obtained by calculatng the mean number of schools registered per minute of survey (this was also done for surveys in 1982–1984 to provide a second index of abundance, and to estimate capelin biomass). Capelin trap catches, small mesh gill net catches, local cod ($n$ = 680) and seabird ($n$ = 2121) stomach collections, and direct observations indicated that capelin were by far the most common pelagic schooling fish occurring in Witless Bay and appearing on echogram traces (Piatt 1987, 1989; Methven and Piatt 1989).

Correlations between whale and capelin abundance were determined using data combined over 5-d intervals to reduce short-term temporal variance (Piatt 1989). The influence of environmental parameters on whale abundance was assessed with stepwise multiple regression (Whitehead 1981). Water temperature profiles, tide ranges, and wind vectors were obtained or calculated as described by Piatt (1987, 1989) and Schneider and Methven (1988).

Estimates of total capelin biomass per survey were calculated for 1982–1985 by multiplying the total number of schools counted on echograms (standardized for survey duration) by the average volume of capelin schools (ca. 525 $m^3$; Zaferman 1972), by the average density of capelin per school (15.7 ± 15%/$m^3$; Zaferman 1972), and by the average weight of capelin in each year (measured from fish collected in traps; Piatt 1987), and extrapolating from the area surveyed hydroacoustically (1.5 $km^2$) to the total study area (30 $km^2$) in which whales were observed.

Estimates of the amount of prey consumed by whales were made as described by Hain et al. (1985) where daily individual basal energy requirements (kcal/day) = 70(body wt. (kg))$^{0.75}$ × capelin energy content (ca. 0.90 kcal/g; Montevecchi and Piatt 1984) × correction factors for (*i*) metabolism beyond basal (2), (*ii*) assimilation efficiency (1.25), and (*iii*) food storage requirements (1.5) (1 cal = 4.1868J). Biomass of whales used in equations were taken from Whitehead (1981): fin, 50 metric tons (t); humpback, 33 t; and minke, 9 t. Total daily capelin consumption was calculated as the sum of requirements of all individual whales seen on a given day (assuming all whales were eating capelin, and discarding duplicate observations).

## Results

### *Behaviour*

A variety of behaviours were exhibited by fin, humpback, and minke whales at Witless Bay. Whales sometimes passed quickly through the study area in a straight line, in a direction parallel to the coast and usually outside of the islands (Fig. 1). This apparent migratory behaviour (Whitehead 1981) was most pronounced outside of the peak period of capelin spawning in each year.

When capelin were locally abundant, whales concentrated in areas preferred by schooling capelin (e.g., near headlands; at the Ledge, a shoal between Gull and Green islands; and at Whale Deep, a trough between Green and Great islands). Foraging by whales was observed directly or inferred from their behaviour (Whitehead 1981). Short bouts of lunge-feeding on shallow capelin schools by humpback and minke whales were observed near shore or near Gull Island in all years. A zigzag searching behaviour typical of foraging humpbacks (Whitehead 1981) was also noted for fin and minke whales temporarily residing in Witless and Mobile bays or making their way slowly along the coast. When both whales and capelin were abundant, large groups of (mostly) humpback whales were seen foraging on capelin aggregations for hours and sometimes over several days. Bouts of intense, coordinated feeding activity by humpbacks (cf. Whitehead 1983) were interspersed with periods of rest (shallow, slow swimming and lolling at the surface). Mixed-species groups of whales were infrequently observed at large capelin aggregations, but different species did not appear to coordinate feeding activities.

TABLE 1. Survey effort and capelin abundance at Witless Bay, Newfoundland, 1982–1985

| | Survey effort | | | Capelin abundance[c] | | |
|---|---|---|---|---|---|---|
| | Total no. of days[a] | No. of boat surveys[b] | Date range | Mean abundance | Mean biomass/d (t) | Max. biomass/d (t) |
| 1982 | 46 (73) | 11 (6) | May 28 – Aug. 9 | 2.3 | 3610 | 6990 |
| 1983 | 61 (80) | 37 (29) | May 28 – Aug. 15 | 0.83 | 949 | 2065 |
| 1984 | 53 (114) | 35 (25) | May 9 – Aug. 30 | 0.11 | 477 | 1160 |
| 1985 | 54 (115) | 29 (29) | May 7 – Aug. 25 | — | 674 | 1555 |
| Overall | 214 (382) | 112 (89) | | 1.08 | 700[d] | 1600[d] |

[a]Number of days on which whale observations were made from Gull Island and (or) the boat; numbers in parentheses are total no. of days observations could have been made (no. of days in date range).
[b]Numbers in parentheses are no. of surveys in which hydroacoustic estimates of capelin abundance were obtained.
[c]Mean abundance is relative abundance calculated from graded echogram traces. (not available for 1985). Capelin biomass was extrapolated from no. of schools encountered per survey. See Study area and methods.
[d]Mean biomass calculated from 1983–1985 surveys only.

TABLE 2. Baleen whale abundance at Witless Bay, Newfoundland, 1982–1985

| | No. of whales | | | | No. of whales/h | | | % whales | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Total | Fin | Humpback | Minke | Fin | Humpback | Minke | Fin | Humpback | Minke |
| 1982 | 181 | 10 | 124 | 47 | 0.19 | 0.71 | 0.49 | 5 | 69 | 26 |
| 1983 | 160 | 20 | 118 | 22 | 0.05 | 1.04 | 0.16 | 12 | 74 | 14 |
| 1984 | 110 | 6 | 69 | 35 | 0.04 | 0.55 | 0.35 | 5 | 63 | 32 |
| 1985 | 124 | 5 | 86 | 33 | 0.14 | 2.11 | 0.81 | 4 | 69 | 27 |
| Overall | 575 | 41 | 397 | 137 | 0.11 | 0.89 | 0.45 | 7 | 69 | 24 |

NOTE: Totals based on total numbers of different whales observed each day after discarding duplicate sightings by different observers. Whales observed per hour of effort calculated using only standardized survey data (see Study area and methods).

*Annual variation in whale and capelin abundance*

Few hydroacoustic surveys were conducted in 1982, and 1985 surveys were not standardized. Bearing these methodological limitations in mind, it appears that capelin abundance progressively declined by an order of magnitude between 1982 and 1984, and increased again in 1985 (Table 1). Observations on the abundance and food habits of capelin predators corroborate the hydroacoustic surveys. For example, the frequency of capelin found in cod, murre, and puffin stomachs declined progressively from 1982 to 1984 ($p < 0.0001$ for all between-year bird comparisons using Kolmogorov–Smirnov tests; Piatt 1987; Methven and Piatt 1989), and the catch per unit effort of cod in gill nets declined from 1982 to 1984 but increased between 1984 and 1985 (J. F. Piatt, unpublished data).

In perfect rank order ($r = 1.0$, df = 2, ns) with variations in capelin abundance, the total number of all whales observed at Witless Bay declined between 1982 and 1984, and increased again in 1985 (Table 2). However, each species exhibited different patterns of variation over the years. For example, capelin abundance declined about 8-fold between 1983 and 1984 and less than half as many fin whales were observed in 1984 as in 1983, although the number observed per hour declined only slightly. Both total number and number observed per hour of humpback whales declined by about half between 1983 and 1984. In contrast, the total number and number observed per hour of minke whales increased about 2-fold between 1983 and 1984.

In numerical terms, humpback whales accounted for 69% (range: 63–74%) of baleen whales observed over all years (Table 2). Minke whales were next most abundant (mean 24%, range 14–27%), followed by fin whales (mean 7%, range 4–12%). Other cetaceans observed included pilot whales (*Globicephala melaena*, 3 observed on July 25, 1982), white-sided dolphins (*Lagenorhynchus acutus*, 10 on June 25, 1982; 6 on July 12, 1982; 15 on July 8, 1983; and 18 on July 26, 1984), and white-beaked dolphins (*Lagenorhynchus albirostris*, 30 on August 21, 1985).

*Seasonal variations in whale and capelin abundance*

Whales were most numerous during peak periods of capelin abundance between late June and late July (Fig. 2). In some years (e.g., 1982 and 1984), humpback and minke whales were also observed over several days well before or after the peak period of inshore capelin abundance (possibly on non-feeding migration through the area). In contrast, fin whales were only seen during days of peak capelin abundance.

Temporal correlations between whale and capelin abundance are shown in Table 3. Fin whale numbers were significantly correlated with capelin in 2 of 4 years, and over all years combined. Both humpback and minke whale numbers were significantly correlated with capelin abundance in all years and overall. Correlations were strongest in years of high capelin abundance. In most years, and overall, there were strong, significant correlations between numbers of fin, humpback, and minke whales; reflecting a high degree of temporal overlap between species.

For the 2 years in which environmental data were also collected (1983 and 1984), variations in total whale abundance were best explained by variations in capelin abundance (Table 4). Addition of environmental parameters to the regression model resulted in only a marginal increase in the proportion of variance explained. Similar results were obtained when each whale species was considered separately.

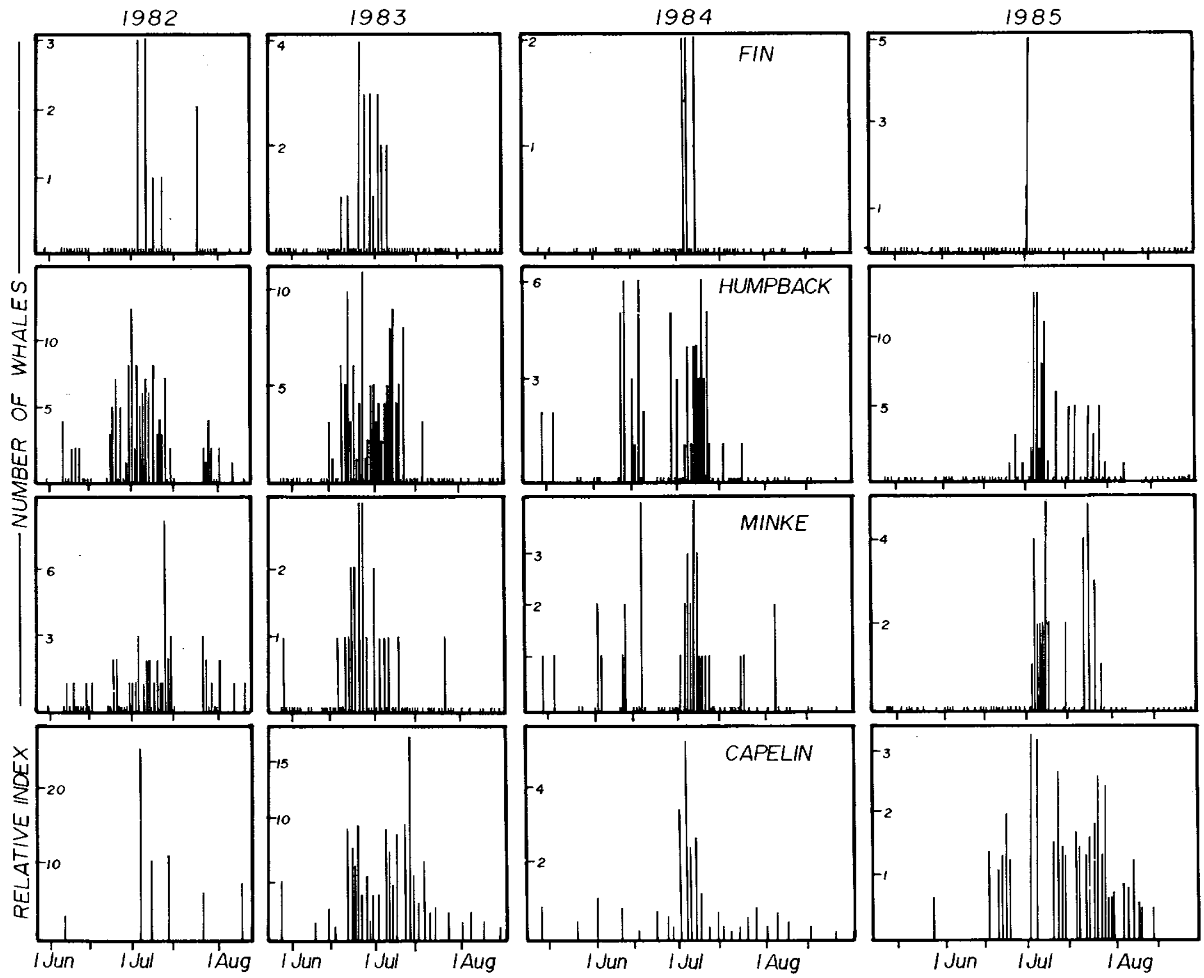


FIG. 2. Seasonal trends in total numbers of fin, humpback, and minke whales observed at Witless Bay, and relative capelin abundance index in 1982–1985. Note that capelin abundance was calculated differently in 1985 (see Study area and methods).

*Capelin consumption*

The total amount of capelin consumed by whales (Table 5) is probably underestimated because whale surveys were not conducted every day, although coverage was almost complete during peak periods of whale and capelin abundance. These calculations suggest that baleen whales took between 60 and 100 t of capelin from Witless Bay in each year, with the greatest consumption on any one day ranging between 5 and 15 t. Humpback whales consumed an average of 79% (range 76–82%) of the total biomass taken by baleen whales. Fin (11%, range 6–18%) and minke (10%, range 5–15%) whales took about equal shares of the remainder.

Total capelin abundance varied daily, reflecting mortality (natural and from predation), and the arrival and departure of schools to and from the spawning area. Thus, the total amount of capelin available to whales over summer cannot be calculated simply as the sum of quantities estimated from surveys on different days. However, the impact of whales on capelin stocks can be assessed by comparing the maximum amount of capelin all whales could consume daily (Table 5) with estimates of maximum and mean daily abundance of capelin in the study area in 1983–1985 (Table 1). On the days of maximum capelin abundance in each summer, all whales consumed only 0.59% (range 0.44–0.89%) of the total capelin biomass available in the study area. Even on days of highest whale abundance, whales consumed only 1.4% of the mean daily biomass of capelin in the study area.

*Habitat distribution*

Although all species were observed inshore, in bays, and offshore (Fig. 1), each species tended to occupy these habitats to a different extent (Fig. 3). Observations were probably biased towards bay habitat because observers on Gull Island were more likely to see whales close to the island (i.e., in the bay). Combined data from all years revealed highly significant differences in habitat use by the three species (overall $\chi^2$ = 32.0, df = 4, $p < 0.0001$). Fin whales tended to occur offshore more than humpback whales ($\chi^2$ = 9.8, df = 2, $p < 0.01$), and minke whales tended to forage closer to shore (particularly near headlands) than did humpback whales ($\chi^2$ = 19.5, df = 2, $p < 0.0001$).

## Discussion

The patterns of whale abundance observed in this study were similar to patterns observed elsewhere in Newfoundland in other years. Humpback whales were numerically dominant at Witless Bay, as they were at Whitehead's coastal (Bay de Verde; Whitehead 1981) and offshore (Southeast Shoal; Whitehead and Glass 1985) study sites. Approximately 2000 humpbacks visit Newfoundland waters during summer

TABLE 3. Spearman rank correlations in abundance between capelin, and fin, humpback, and minke whales in 1982–1985[a]

| | Variable | Survey | $n$ | Fin | Humpback | Minke |
|---|---|---|---|---|---|---|
| 1982 | Capelin abundance | B | 6 | 0.65 | 0.86* | 0.94** |
| | | T | 6 | 0.55 | 0.77 | 0.67 |
| | Fin | B | 6 | | 0.77 | 0.65 |
| | | T | 17 | | 0.71** | 0.74*** |
| | Humpback | B | 6 | | | 0.59 |
| | | T | 17 | | | 0.83**** |
| 1983 | Capelin abundance | B | 16 | 0.58* | 0.66** | 0.74** |
| | | T | 16 | 0.50* | 0.61* | 0.61* |
| | Fin | B | 16 | | 0.61* | 0.76*** |
| | | T | 21 | | 0.80**** | 0.78**** |
| | Humpback | B | 16 | | | 0.75*** |
| | | T | 21 | | | 0.81**** |
| 1984 | Capelin abundance | B | 18 | 0.40 | 0.53* | 0.50* |
| | | T | 18 | 0.55* | 0.19 | 0.50* |
| | Fin | B | 18 | | 0.38 | 0.44 |
| | | T | 24 | | 0.45* | 0.54* |
| | Humpback | B | 18 | | | 0.78*** |
| | | T | 24 | | | 0.66*** |
| 1985 | Capelin abundance | I | 10 | 0.52 | 0.89**** | 0.73** |
| | Fin | I | 19 | | 0.42 | 0.39 |
| | Humpback | I | 19 | | | 0.75*** |
| Total | Capelin abundance | B | 50 | 0.43** | 0.45** | 0.52**** |
| | | T | 50 | 0.60**** | 0.51**** | 0.54**** |
| | Fin | B | 59 | | 0.45*** | 0.48*** |
| | | T | 81 | | 0.61**** | 0.60**** |
| | Humpback | B | 59 | | | 0.65**** |
| | | T | 81 | | | 0.76**** |

[a]Correlations tested using data from different survey types (see Study area and methods): B, boat surveys (standardized); T, total observations (not standardized); I, standard surveys from Gull Island. Capelin abundance from hydroacoustic surveys (see Study area and methods).

*$p < 0.05$.

**$p < 0.01$.

***$p < 0.001$.

****$p < 0.0001$.

(Whitehead 1981). Given the total number of humpbacks we observed, and assuming that the average humpback visit to Witless Bay lasted only 1–2 days (Whitehead et al. 1980, 1982), then we conclude that about 50–100 different humpbacks or 2.5–5% of the Northwest Atlantic population passed through Witless Bay during their northward feeding migration in each year. Similar numbers of humpbacks were observed to pass along the tip of the Bay de Verde Peninsula (ca. 120 km NW of Witless Bay) in 1978–1980 (Whitehead et al. 1982).

Although fin whales may be as abundant as humpbacks in Newfoundland waters, they were an order of magnitude less common than humpbacks at Witless Bay. This disparity might be explained by two factors. (*i*) Although the Newfoundland population of fin whales was estimated at ca. 2000 individuals in 1972 (Allen 1973), it may have declined since then (Lynch and Whitehead 1984; Whitehead and Carscadden 1985). The ratio of fins to humpbacks observed over a large coastal and offshore area of Newfoundland declined from 0.74 in 1976 to 0.04 and 0.25 in 1982 and 1983, respectively (Lynch and Whitehead 1984). Witless Bay fin/humpback ratios in 1982 (0.08) and 1983 (0.19) were similar to those found by Lynch and Whitehead in those years, and remained low in 1984 (0.09) and 1985 (0.06) at Witless Bay. (*ii*) Fin whales prefer to feed offshore or in the middle of large deep-water bays (Perkins and Whitehead 1977; Parsons and Brownlie 1981), and hence Witless Bay may not have been an attractive feeding area.

Minke whale populations appear to be stable in Newfoundland (Whitehead and Carscadden 1985), and the numbers observed at Witless Bay were typical for inshore areas (Perkins and Whitehead 1977; Whitehead 1981). There were no consistent variations in the ratio of minkes to humpbacks in Newfoundland between 1976 and 1983 (average ratio 0.39; Lynch and Whitehead 1984) and similar ratios were observed at Witless Bay between 1982 and 1985 (overall ratio 0.35, range 0.19–0.51).

The most important factor determining seasonal patterns of abundance of baleen whales at Witless Bay appeared to be capelin abundance. Significant seasonal correlations between humpback or fin whale numbers and prey abundance have been reported previously in Newfoundland (Whitehead 1981) and on George's Bank (Paine et al. 1986). However, we are not aware of any other studies that have demonstrated significant correlations between minke whales and their prey.

Environmental conditions did not appear to directly influence whale abundance at Witless Bay. This might be expected because their large size and heavy insulation buffer them

TABLE 4. Stepwise multiple regressions of baleen whales observed per effort with environmental parameters at Witless Bay in 1983–1984

| Model | df | $r^2$ | $F$ | $p$ |
|---|---|---|---|---|
| 1983 | | | | |
| Capelin | 1,15 | 0.63 | 24.05 | 0.0002 |
| Capelin + | 5,15 | 0.69 | 4.41 | 0.02 |
| Capelin | | | 20.33 | 0.0011 |
| Date | | | 0.33 | 0.86 |
| Tidal range | | | 1.70 | 0.22 |
| Water temperature | | | 0.01 | 0.93 |
| Wind vector | | | 0.03 | 0.86 |
| 1984 | | | | |
| Capelin | 1,14 | 0.63 | 21.86 | 0.0004 |
| Capelin + | 5,14 | 0.72 | 4.67 | 0.02 |
| Capelin | | | 9.62 | 0.013 |
| Date | | | 1.28 | 0.29 |
| Tidal range | | | 0.02 | 0.88 |
| Water temperature | | | 1.34 | 0.28 |
| Wind vector | | | 2.43 | 0.16 |

NOTE: Model results using capelin abundance alone, and capelin plus four environmental variables.

TABLE 5. Potential consumption of capelin by baleen whales at Witless Bay, Newfoundland, 1982–1985

| | Max. daily (t/day) | Total (t/season) | % consumption | | |
|---|---|---|---|---|---|
| | | | Fin | Humpback | Minke |
| 1982 | 8.0 | 99.9 | 9 | 80 | 11 |
| 1983 | 11.3 | 98.7 | 18 | 77 | 5 |
| 1984 | 5.1 | 58.1 | 9 | 76 | 15 |
| 1985 | 13.7 | 67.7 | 6 | 82 | 12 |
| Mean | 9.5 | 81.1 | 11 | 79 | 10 |

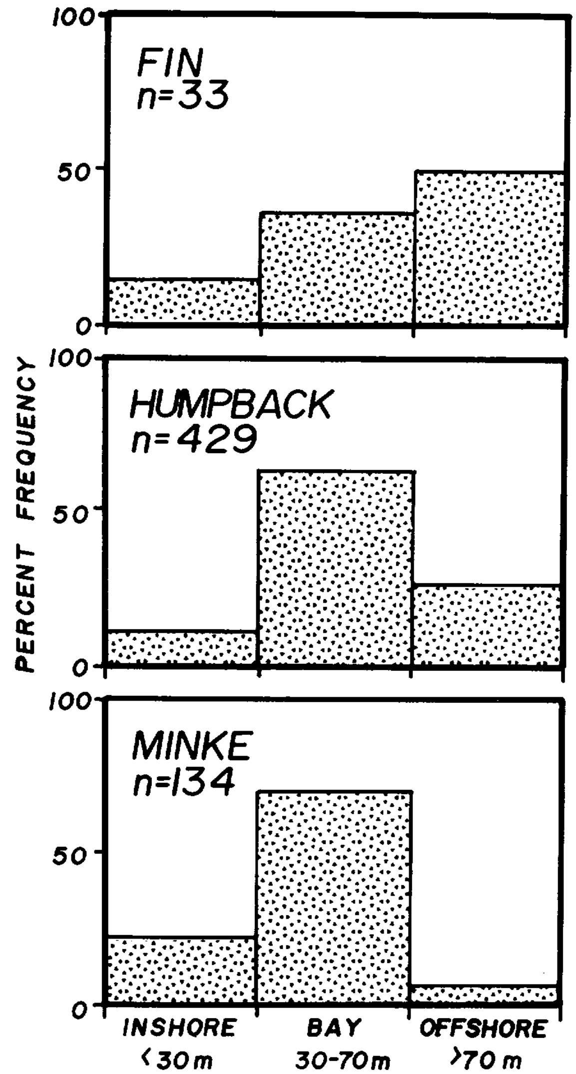


FIG. 3. Frequency of occurrence of fin, humpback, and minke whales in different habitats at Witless Bay. Data combined for 1982–1985.

against environmental extremes (Whitehead 1981). However, direct relationships between wind-driven coastal upwelling, water temperatures, tides, and capelin behaviour have been demonstrated (Piatt 1987; Schneider and Methven 1988) and oceanographic conditions influencing capelin must indirectly influence whale behaviour as well. More fine-scale studies will be required to resolve these relationships.

Interannual variations in whale abundance also appeared to be a function of inshore capelin abundance, but the relationship may be complex and different for each of the species considered. The abundance of whales inshore also depends on the relative abundance of capelin offshore (Whitehead and Carscadden 1985). For example, a large increase in the numbers of baleen whales seen inshore in the late 1970's probably resulted from a decline in offshore capelin stocks rather than an increase in inshore stocks (Whitehead and Carscadden 1985).

Different species may respond differently to annual variations in capelin abundance. In all years at Witless Bay, fin whales were only seen during days of extremely high capelin abundance. Whereas humpback numbers decreased, minke numbers increased markedly when capelin abundance declined between 1983 and 1984. These results suggest that each species may have differing capelin (prey) density preferences (fin > humpback > minke).

Estimates of the impact of whale predation on fish stocks have been made for several large regions. Winters (1975) calculated that baleen whales in Newfoundland consumed about 400 000 t of capelin annually, about equivalent to capelin consumption by either seabirds, seals, or man, but substantially less than consumption by cod. Hain et al. (1985) calculated that cetaceans on George's Bank consumed about 480 000 t of food/year, and concluded that cetaceans were major predators on the banks and shelf edge, and potential competitors with fish and humans for food resources.

Our analysis of the much smaller system at Witless Bay suggests that the overall impact of baleen whales on capelin stocks there was minimal. Capelin aggregations are typically composed of tens or hundreds of individual capelin schools, and 5–20 t of capelin may be found in a single aggregation (Zaferman 1972; Piatt 1989). Dozens of such aggregations were encountered on survey transects during peak days of capelin abundance at Witless Bay. Purse seiners and beach traps in the area often captured 1–10 t of capelin in single sets (J.F.P., personal observation), and did so repeatedly through the capelin fishing season (ca. 2 weeks). Thus, our estimates of maximum capelin abundance on peak days were conservative, and it is probable that tens of thousands of tons of capelin were locally available to whales over the capelin spawning period. In contrast to whales, the large breeding population of seabirds at Witless Bay may take more capelin in one day (ca. 160 t, Brown and Nettleship 1984; Cairns et al. 1987) than all whales did in a season (ca. 60 – 100 t).

Calculations of total consumption may be misleading, however, because they tell us little about actual foraging requirements and predator – prey relationships. It has been suggested that large whales require some minimum prey biomass density for efficient foraging (Brodie 1977; Kenney et al. 1986). At Witless Bay, baleen whales were abundant only during peak periods of capelin abundance whereas seabirds and cod foraged locally over longer time periods (Piatt 1987, 1989; Methven and Piatt 1989). The role of prey density, as opposed to abundance, in shaping food-web relationships needs to be evaluated.

There was a consistently high degree of temporal overlap in the use of Witless Bay by the three whale species. This has been observed elsewhere (e.g., Perkins and Whitehead 1977; Lynch and Whitehead 1984; Kenney et al. 1986) and has frequently led to speculation that coexisting baleen whales may compete for food (Mitchell 1975; Whitehead 1981; Lynch and Whitehead 1984). However, the overall amount of food at Witless Bay appeared to be superabundant and, furthermore, competition was probably reduced because fin whales fed more offshore, and minkes fed more inshore, than humpback whales. Perkins and Whitehead (1977) noted similar spatial segregation of fin, humpback, and minke whales off northern Newfoundland. Also, these whales probably feed at different depths in the water column (fin > humpback > minke; Whitehead 1981). Nonetheless, resource competition could occur for high density prey schools and spatial segregation may result partly from interference competition (Lynch and Whitehead 1984). Neither form of competition can be assessed without more detailed studies of whale foraging behaviour in relation to their prey.

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